THE BIOLOGY OF RUSTS OF THE GENUS UREDINOPSIS

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As PART of a contribution towards a monograph on *Uredinopsis* I have recently presented an account of its taxonomy and geographical distribution (4). The paper now offered is devoted, except for a short section on economic considerations, to topics on the biology of Uredinopsis rusts. These topics comprise (1) hosts, (2) life history studies, (3) developmental periods, (4) habits of spore production, (5) host restrictions.

I. HOSTS

Ferns and ferns only serve as hosts for the diploid generation of all known species of rusts belonging to the genus *Uredinopsis*. These are restricted to *Osmunda* of the family Osmundaceae and twelve genera of the family Polypodiaceae. The subfamilies and genera represented in the latter are as follows: WOODSIEAE — *Cystopteris, Matteuccia, Onoclea, Woodsia;* ASPIDIEAE — *Dryopteris;* ASPLENIEAE — *Athyrium, Blechnum, Woodwardia;* PTERIDEAE — *Adiantum, Cheilanthes, Pellaea, Pteridium.*

In view of the fact that *Uredinopsis,* partly because of its occurrence on ferns, is generally considered to be one of the most primitive of existing rust genera, the finding of a species on *Osmunda* would seem at first sight to be of peculiar interest, because the Osmundaceae on both historical and morphological grounds were evidently antecedent to the Polypodiaceae. But *Uredinopsis Osmundae,* the rust in question, exhibits some of the more specialized features of the genus and none that are uniquely generalized. Apparently it is less primitive than certain species on polypodiaceous hosts. Hence, there is no reason to believe that any particular phylogenetic significance attaches to the one known species of *Uredinopsis* on *Osmunda.*

Quite in contrast to the generally rather long-lived fronds of the ferns susceptible to Milesia rusts, those that serve as hosts for Uredinopsis rusts are strictly seasonal, dying at the end of their single growing period. This means that all their spore production must take place in the one season; there can be none in the following spring as is true for most species of *Milesia.* Compensation for this difference, however, is found in the

circumstance that many species of *Uredinopsis* are provided with uredial overwintering spores (*amphispores*) in addition to their ordinary urediospores, thus making possible the perpetuation of those species on their fern hosts alone without any intervening development of the haploid phase on alternate hosts.

Alternate hosts have been demonstrated for sixteen species of *Uredinopsis* and for many of these the experimentation has been satisfactorily complete. In every instance they have proved to be species of *Abies* and it is reasonable to assume that *Abies* is almost certainly the actual or potential alternate host for all species of *Uredinopsis*. So far two species only are known to occur outside the range of *Abies*, but quite possibly others may yet be added to the list — species at present undiscovered, or known species such *U. glabra*. Of the two species referred to, one of them, *U. macrosperma*, is almost cosmopolitan, following its fern hosts on the one hand to their northerly range and on the other hand reaching down through the tropics to the South Temperate Zone. Beyond the southern limits of *Abies* the growth habits of the fern hosts easily make possible an unbroken continuance of the diploid phase of the rust. The other, *U. Mayoriana*, is known from Colombia only, far removed from any existing species of *Abies*. Whether or not it originated there we do not know. But if it did *Abies* must at one time have grown in Colombia or an adjacent tropical area, or it is an evolution from the diploid phase of some other species of *Uredinopsis*, or, most improbable of all, it has an alternate host other than *Abies*. In his discussion of the same phenomenon pertaining to certain species of *Milesia*, Faull (2) expresses preference for the second hypothesis.

II. LIFE HISTORY STUDIES

The first successful studies of the life history of any rust fungus of the genus *Uredinopsis* were made by Fraser; the species studied was *U. mirabilis* (Peck) Magnus. Impressed by the prevalent field association of *Peridermium balsameum* Peck on *Abies balsamea* (L.) Mill. and *U. mirabilis* on *Onoclea sensibilis* L., Professor Fraser (5) made exploratory tests in the summer of 1911 to find out whether or not these might be the haploid and diploid phases, respectively, of the same species. He inoculated several pot-grown plants of *O. sensibilis* in a greenhouse with aeciospores of what appeared to be the appropriate *P. balsameum*. Infection resulted promptly; within 8 to 11 days the inoculated fronds bore mature uredia of *U. mirabilis*. The controls remained free from infection; but, as there was a possibility of contamination, a more exacting series of experiments (7) was carried out in the summer of 1913.

Overwintered teliospores of *U. mirabilis* were then used to inoculate pot-grown plants of *Abies balsamea*. Spermogonia were present 8 to 11 days later and aecia 16 to 18 days after inoculation. Some of the culturally produced aeciospores were sown next on *O. sensibilis* and various other ferns; infection resulted on *O. sensibilis* but the others proved to be immune. This work rounded out Fraser's study of the life history of *U. mirabilis;* and in addition to demonstrating its host relationships, the experiment gave clear indication according to Fraser that "*Uredinopsis mirabilis* is a distinct species." Meanwhile, in the intervening year, Fraser (6) tested four recognized species of *Uredinopsis* by inoculating *Abies balsamea* with their overwintered teliospores, as follows: (1) *U. Struthiopteridis* Störmer from *Matteuccia Struthiopteris* (L.) Todaro; (2) *U. Osmundae* Magnus from *Osmunda Claytoniana* L.; (3) *U. mirabilis* (Peck) Magnus from *Onoclea sensibilis* L.; (4) *U. Phegopteridis* Arthur from *Dryopteris Linnaeana* C. Chr. In each case infection resulted, the aecia being those of what apparently answered to Peck's *Peridermium balsameum*. Fraser also inoculated *Dryopteris Thelypteris* var. *pubescens* (Lawson) A. R. Prince with aeciospores of the "*Peridermium balsameum*" which field associations indicated to be those of *U. Atkinsonii*. A meager infection occurred on one of the three plants used for the experiment and none on the others.

Two other contributions on the life histories of Uredinopsis rusts quickly followed, one by Klebahn (12) on *U. Struthiopteridis* in Europe, and the other by Weir and Hubert (14) on *U. macrosperma* in western North America. Using telial material from *Matteuccia Struthiopteris,* Klebahn obtained abundant infection on *Abies alba* Mill. Then sowing the culturally produced aeciospores back to *M. Struthiopteris,* infection followed accompanied with a profuse crop of ordinary uredia. By other suitable experiments Klebahn correctly interpreted for the first time the nature of amphispores.

Weir and Hubert's investigation of the life history of *Uredinopsis macrosperma,* though fragmentary, was significant. The inoculum used consisted of aeciospores from second year needles of *Abies grandis* Lindl. and was collected at Priest River, Idaho in the neighborhood of bracken ferns heavily rusted with *U. macrosperma*. The cultures were conducted on two potted plants of *Pteridium aquilinum* var. *lanuginosum* (Bong.) Fernald in a greenhouse at Missoula, Montana. Infection resulted on one of the ferns and the urediospores proved to be those of *U. macrosperma*. Obviously their work should be repeated and extended, but the results of their experiment lead to the reasonable conclusion that *U. macrosperma* alternates between *Pteridium* and *Abies*. I have had the

opportunity of examining part of their unused inoculum and also uredia from the rusted fronds of their experimental fern. The former unquestionably corresponds to *Peridermium pseudo-balsameum* (D. & H.) Arthur & Kern and the latter to the uredial fructifications of *U. macrosperma.*

The remaining studies on the life histories of Uredinopsis rusts recorded in the literature we owe to the excellent work of Kamei (8, 9) in Japan. Beginning with telial materials he has cultured the following species as indicated: (1) *Uredinopsis Kameiana* Faull from *Pteridium aquilinum* var. *japonicum* Nakai to *Abies Mayriana* Miyabe & Kudô and then back to the fern host; (2) *U. Woodsiae* Kamei from *Woodsia polystichoides* var. *nudiuscula* Hook. to *Abies Mayriana;* (3) *U. Athyrii* Kamei to *Abies Mayriana;* (4) *U. hirosakiensis* Kamei & Hirat. f. from *Dryopteris Thelypteris* var. *pubescens* (Lawson) A. R. Prince to *Abies Mayriana;* (5) *U. intermedia* Kamei from *Athyrium thelypteroides* (Michx.) Desv. and *A. pterorachis* Christ to *Abies Mayriana;* (6) *U. ossaeiformis* Kamei from *Dryopteris dilatata* var. *oblonga* Takeda, and *D. monticola* (Mak.) C. Chr. to *Abies Mayriana, A. firma* Sieb. & Zucc. and *A. sachalinensis* (Schm.) Mast.; (7) *U. filicina* (Niessl) Magnus from *Dryopteris Phegopteris* (L.) C. Chr. to *Abies Mayriana.*

My own researches have been concerned with six species of *Uredinopsis,* namely, (1) *U. longimucronata* Faull from *Athyrium angustum* (Willd.) Presl, (2) *U. Osmundae* Magnus from *Osmunda cinnamomea* L., *O. Claytoniana* L. and *O. regalis* var. *spectabilis* (Willd.) A. Gray, (3) *U. mirabilis* (Peck) Magnus from *Onoclea sensibilis* L., (4) *U. Phegopteridis* Arthur from *Dryopteris Linnaeana* C. Chr., (5) *U. Struthiopteridis* Störmer from *Matteuccia Struthiopteris* (L.) Todaro, (6) *U. ceratophora* Faull from *Cystopteris bulbifera* (L.) Bernh. The experiments were conducted at the University of Toronto Field Laboratory of Forest Pathology at Bear Island, Lake Timagami, Timagami Forest Reserve, Ontario, and the work was completed at the Arnold Arboretum, Harvard University, Jamaica Plain, Massachusetts. In the former locality all of the rusts mentioned, except *U. ceratophora,* are readily obtainable in ample quantities on their respective fern hosts; and the coniferous host, *Abies balsamea,* abounds there. Teliosporic material of *U. ceratophora* was collected by Dr. Lillian M. Hunter at Bradford, Ontario, where it seems to be frequent.

Studies on each of the species began with the telial stage. Teliosporic material was collected in the fall; part of it was overwintered in net bags out of doors, and part, slightly moistened occasionally, in a refrigerator in the laboratory. At the time the new needles of *Abies* were expanding

overwintered fronds bearing teliospores were brought into the laboratory, and, so as to force spore germination, they were placed between folds of wet paper or laid on damp sphagnum moss in large loosely covered cans. Small test pieces were also kept under moist conditions in Petri dishes to afford greater ease of observation. Close watch was kept for the emergence of basidia and the first formation of basidiospores. As soon as basidiospores were freely appearing the material was ready for making inoculations. In setting up an experiment a portion of a frond carrying inoculum was either laid, abaxial surface down, directly on the foliage of a small branch of the host to be inoculated, or it was first prepared for easier handling and greater economy in use by laying it between two strips of galvanized wire netting, separated from the upper strip by a piece of wet absorbent paper. The chosen branch by way of its preparation was sprayed with water from an atomizer and so flexed that its lower face would come in juxtaposition with the basidial-bearing face of the piece of frond. A celluloid cylinder about six inches long by two inches in diameter (E. E. Hubert — Celluloid cylinders for inoculation chambers. Phytopath. **6:** 447–450. 1916) plugged at one end with wet sphagnum was then slipped over the branch and its adjustment completed by packing its proximal end around the branch in its axis with wet sphagnum. Whenever necessary the branch was propped to keep it as nearly as possible in a horizontal position until the tube was finally removed some days later. The experiment was visited daily as long as the tube was in use, and the sphagnum plugs were kept wet by the addition of water as needed. Similar technique was employed in subsequent inoculations of ferns except that in some instances the inoculum consisted of a suspension of spores in water which was sprayed on the fronds.

Summaries of the experiments are recorded below in Tables 1 to 22. The following data, where pertinent, constitute a part of each table:

(1) The cultures were made under properly controlled conditions.

(2) All controls (unless otherwise stated) remained free from infection.

(3) Infections on *Abies* resulted on needles of the current season only.

(4) Inoculations on *Abies* were made soon after the unfolding of the new needles.

(5) Detailed data of the experiments, in tabular form, are filed in the J. H. Faull Herbarium.

(6) Representative culture materials of the positive experiments are filed in the J. H. Faull Herbarium under the numbers indicated in the Tables.

1. **Uredinopsis Struthiopteridis** Störmer

Uredinopsis Struthiopteridis occurs in both hemispheres throughout the range of its fern host, *Matteuccia Struthiopteris* (L.) Todaro. In America Fraser (6) demonstrated by cultures that it can be carried over to *Abies balsamea*. Conversely, he secured infection on the fern host by sowing aeciospores from the balsam fir "collected beside ferns of *Onoclea Struthiopteris* that were badly rusted the previous season." Other sowings of aeciospores from the same source were made on *Onoclea sensibilis, Dryopteris Linnaeana* and *Osmunda Claytoniana;* but the results were negative. In Europe Klebahn (12) similarly demonstrated that *U. Struthiopteridis* can be cultured on *Abies alba*. Then, by using the culturally produced aeciospores as inoculum, he carried it back to the fern host. He also obtained infection of the fern by inoculating it with the amphispores of *U. Struthiopteridis*. Finally in Japan, Kamei (10) was successful in culturing *U. Struthiopteridis* on *Abies Mayriana*.

Summaries of my own experiments are recorded in Tables 1 and 2. They were fully confirmatory and at the same time they served the purpose of providing necessary comparative materials. As an important part of the work, culture tests were made on *Athyrium angustum* (Willd.) Presl, *Dryopteris Linnaeana* C. Chr., *Onoclea sensibilis* L. and *Osmunda Claytoniana* L. These were shown to be immune to *U. Struthiopteridis*.

TABLE 1.

CULTURES OF UREDINOPSIS STRUTHIOPTERIDIS FROM MATTEUCCIA STRUTHIOPTERIS TO ABIES BALSAMEA

1. *Fifty-four inoculation experiments* were made; forty-nine gave *positive* results.
2. The dates of inoculation ranged from June 20 to July 7.
3. Yellowing of the needles appeared 9 to 11 days after inoculation. *The average was 10 days.*
4. The spermogonia were first observed 10 to 15 days after inoculation. *The average was 12 days.*
5. The peridermia were first observed 19 to 24 days after inoculation. *The average was 21 days.*
6. The peridermia usually began to rupture the day following their first appearance.
7. The production of peridermia was practically completed within 30 days after inoculation. *The average was about 26 days.*
8. The number of infected needles with peridermia varied from 2 to 162. *The average was 37.*
9. J. H. Faull Herbarium nos. 7732–7743 and 8486.

TABLE 2.

CULTURES OF UREDINOPSIS STRUTHIOPTERIDIS FROM ABIES BALSAMEA TO VARIOUS FERNS, USING AS INOCULUM AECIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 1.

A. *From Abies balsamea to Matteuccia Struthiopteris*

1. *Six inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 14 to July 28.
3. Mature uredia were first observed 10 to 11 days after inoculation.
4. The experiments were harvested 13 to 28 days after inoculation. *The average was 17 days.*
5. The approximate number of uredia present at the time of harvesting varied from 60 to 200. *The average was 138.*
6. J. H. Faull Herbarium nos. 7744–7747.

B. *From Abies balsamea to Athyrium angustum*

1. *Six inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 18 to July 27.
3. The experiments were harvested about 30 days after inoculation.

C. *From Abies balsamea to Dryopteris Linnaeana*

1. *Six inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 15 to July 25.
3. The experiments were harvested about 31 days after inoculation.

D. *From Abies balsamea to Onoclea sensibilis*

1. *Six inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 15 to July 23.
3. The experiments were harvested about 32 days after inoculation.

E. *From Abies balsamea to Osmunda Claytoniana*

1. *Six inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 22 to July 24.
3. The experiments were harvested about 30 days after inoculation.

2. **Uredinopsis mirabilis** (Peck) Magnus

Uredinopsis mirabilis has been collected throughout almost the entire range of *Onoclea sensibilis* L. in North America, and is very common on that host. It has also been found on *O. sensibilis* forma *obtusilobata* (Schk.) Gilbert. It is of further interest to note that a collection was made on *O. sensibilis* in a garden near London, England, where presumably it has been introduced along with its host. *Onoclea sensibilis*

is recognized as occurring naturally in eastern Asia; but so far there are no records of the rust from that part of the world.

Fraser's demonstrations (5, 6, 7) that *U. mirabilis* alternates between *Abies balsamea* and *Onoclea sensibilis* were complete. He also made an important contribution by showing that *U. mirabilis* apparently does not infect *Athyrium angustum, Dryopteris Linnaeana, D. Thelypteris* var. *pubescens, Osmunda Claytoniana* nor *O. regalis* var. *spectabilis*.

My own culture experiments, summaries of which are recorded in Tables 3 and 4, entirely confirm Fraser's findings on the life history of *U. mirabilis*. They have likewise shown that it does not cause infection of *Athyrium angustum* (Willd.) Presl, *Dryopteris Linnaeana* C. Chr., *Matteuccia Struthiopteris* (L.) Todaro, *Osmunda Claytoniana* L.

TABLE 3.

CULTURES OF UREDINOPSIS MIRABILIS
FROM ONOCLEA SENSIBILIS TO ABIES BALSAMEA

1. *Forty-four inoculation experiments* were made; thirty-nine gave *positive* results.
2. The dates of inoculation ranged from June 19 to July 7.
3. Yellowing of the needles appeared 9 to 16 days after inoculation. *The average was 12 days.*
4. The spermogonia were first observed 10 to 15 days after inoculation. *The average was 12 days.*
5. The peridermia were first observed 21 to 28 days after inoculation. *The average was 23 days.*
6. The peridermia usually began to rupture the second day following their first appearance.
7. The production of peridermia was practically completed within 40 days after inoculation. *The average was 32 days.*
8. The number of infected needles with peridermia varied from 1 to 91. *The average was 27.*
9. J. H. Faull Herbarium nos. 7696–7706 and 8494–8496.

TABLE 4.

CULTURES OF UREDINOPSIS MIRABILIS
FROM ABIES BALSAMEA TO VARIOUS FERNS, USING AS INOCULUM AECIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 3.

A. *From Abies balsamea to Onoclea sensibilis*

1. *Six inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 18 to July 31.
3. The uredia were first observed 8 to 9 days after inoculation.

4. The experiments were harvested 9 to 13 days after inoculation. *The average was 11 days.*
5. The approximate number of uredia present at the time of harvesting varied from 200 to 500. *The average was 350.*
6. J. H. Faull Herbarium nos. 7707–7712.

B. *From Abies balsamea to Athyrium angustum*

1. *Four inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 23 to July 29.
3. The experiments were harvested about 29 days after inoculation.

C. *From Abies balsamea to Dryopteris Linnaeana*

1. *Two inoculation experiments* were made; both gave *negative* results.
2. The dates of inoculation ranged from July 25 to July 29.
3. The experiments were harvested about 27 days after inoculation.

D. *From Abies balsamea to Matteuccia Struthiopteris*

1. *Five inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 18 to July 31.
3. The experiments were harvested about 29 days after inoculation.

E. *From Abies balsamea to Osmunda Claytoniana*

1. *Three inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 18 to July 25.
3. The experiments were harvested about 30 days after inoculation.

3. **Uredinopsis longimucronata** Faull.

Uredinopsis longimucronata has its diploid phase on *Athyrium angustum* (Willd.) Presl. Heretofore this rust has passed under the name *U. Atkinsonii* Magnus, a rust described from *Dryopteris Thelypteris* var. *pubescens* (Lawson) A. R. Prince. Faull (3), however, has decided that *U. longimucronata* is distinct from *U. Atkinsonii* because there are fairly constant, though small, morphological distinctions between the two rusts, and because efforts have failed to secure infection of *D. Thelypteris* var. *pubescens* through the use of culturally produced aeciospores of *U. longimucronata* as inoculum. In any case, whatever may be the fate of *U. longimucronata* at the hands of taxonomists, this is the first time that it has been made the subject of life history investigation. It has been successfully carried from *Athyrium angustum* to *Abies balsamea* and then back to *A. angustum*. On the latter, both ordinary urediospores and teliospores were formed. Tests have also shown that it does not cause infection of *Cystopteris bulbifera* (L.)

Bernh., *C. fragilis* (L.) Bernh. *Dryopteris Linnaeana* C. Chr., *D. Thelypteris* var. *pubescens* (Lawson) A. R. Prince, *Matteuccia Struthiopteris* (L.) Todaro, *Onoclea sensibilis* L., *Osmunda Claytoniana* L. Summaries of the experiments are recorded in Tables 5 and 6.

TABLE 5.

CULTURES OF UREDINOPSIS LONGIMUCRONATA FROM ATHYRIUM ANGUSTUM TO ABIES BALSAMEA

1. *Sixty inoculation experiments* were made; fifty-three gave *positive* results.
2. The dates of inoculation ranged from June 10 to July 6.
3. Yellowing of the needles appeared 9 to 17 days after inoculation. *The average was 11 days.*
4. The spermogonia were first observed 9 to 18 days after inoculation. *The average was 12 days.*
5. The peridermia were first observed 17 to 25 days after inoculation. *The average was 20 days.*
6. The peridermia usually began to rupture the second day following their first appearance.
7. The production of the peridermia was practically completed within 41 days after inoculation. *The average was about 30 days.*
8. The number of infected needles with peridermia varied from 1 to 143. *The average was 52.*
9. J. H. Faull Herbarium nos. 7751–7753 and 8472–8481.

TABLE 6.

CULTURES OF UREDINOPSIS LONGIMUCRONATA FROM ABIES BALSAMEA TO VARIOUS FERNS, USING AS INOCULUM AECIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 5.

A. *From Abies balsamea to Athyrium angustum*

1. *Eleven inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 9 to July 21.
3. Mature uredia were first observed 16 to 30 days after inoculation. *The average was 23 days.*
4. The experiments were harvested 22 to 34 days after inoculation. *The average was 28 days.*
5. The approximate number of uredia present at the time of harvesting varied from 0 to 450. *The average was 88.* In one experiment uredia were absent but telia were present.
6. J. H. Faull Herbarium nos. 7754 and 8482–8485.

B. *From Abies balsamea to Cystopteris bulbifera*

1. *Two inoculation experiments* were made; both gave *negative* results.
2. The date of inoculation was July 12.
3. The experiments were harvested 50 days after inoculation.

C. *From Abies balsamea to Cystopteris fragilis*

1. *One inoculation experiment* was made; it gave *negative* results.
2. The date of inoculation was July 12.
3. The experiment was harvested 50 days after inoculation.

D. *From Abies balsamea to Dryopteris Linnaeana*

1. *Seven inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 9 to July 18.
3. The experiments were harvested 30 to 50 days after inoculation.

E. *From Abies balsamea to Dryopteris Thelypteris var. pubescens*

1. *Four inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 12 to July 21.
3. The experiments were harvested 44 to 53 days after inoculation.

F. *From Abies balsamea to Matteuccia Struthiopteris*

1. *Four inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 11 to July 21.
3. The experiments were harvested 48 to 51 days after inoculation.

G. *From Abies balsamea to Onoclea sensibilis*

1. *Five inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 9 to July 21.
3. The experiments were harvested 27 to 51 days after inoculation.

H. *From Abies balsamea to Osmunda Claytoniana*

1. *Seven inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 7 to July 18.
3. The experiments were harvested 36 to 51 days after inoculation.

4. **Uredinopsis Phegopteridis** Arthur

Fraser (6) included *Uredinopsis Phegopteridis* in his life history studies of *Uredinopsis,* although his work on that species was fragmentary. He suspended teliosporic material "in the usual way" above *Abies balsamea* and a meager infection followed — "about twenty of the young leaves bearing aecia." Fraser's work has been repeated here and the experimentation extended to include reverse inoculations on the fern host with the culturally produced aeciospores and also tests on the

resistance of several other ferns. In the experiments, as summarized in Tables 7 and 8, abundant crops of aecia resulted from inoculations on *Abies balsamea;* and on sowing the aeciospores back on *Dryopteris Linnaeana* C. Chr., profuse crops of uredia developed within a surprisingly short time. Cultures also showed that the following ferns are immune to *U. Phegopteridis — Athyrium angustum* (Willd.) Presl, *Matteuccia Struthiopteris* (L.) Todaro, *Onoclea sensibilis* L., *Osmunda Claytoniana* L.

TABLE 7.

CULTURES OF UREDINOPSIS PHEGOPTERIDIS FROM DRYOPTERIS LINNAEANA TO ABIES BALSAMEA

1. *Seventeen inoculation experiments* were made; fourteen gave *positive* results.
2. The dates of inoculation ranged from June 14 to July 2.
3. Yellowing of the needles appeared 10 to 15 days after inoculation. *The average was 12 days.*
4. The spermogonia were first observed 11 to 15 days after inoculation. *The average was 13 days.*
5. The peridermia were first observed 21 to 23 days after inoculation. *The average was 23 days.*
6. The peridermia usually began to rupture the second day following their first appearance.
7. The production of peridermia was practically completed within 35 days after inoculation. *The average was about 28 days.*
8. The number of infected needles with peridermia varied from 8 to 72. *The average was 34.*
9. J. H. Faull Herbarium nos. 7748 and 8488–8493.

TABLE 8.

CULTURES OF UREDINOPSIS PHEGOPTERIDIS FROM ABIES BALSAMEA TO VARIOUS FERNS, USING AS INOCULUM AECIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 7.

A. *From Abies balsamea to Dryopteris Linnaeana*

1. *Three inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 26 to July 31.
3. Mature uredia were first observed 7 to 8 days after inoculation.
4. The experiments were harvested 7 to 12 days after inoculation.
5. The approximate number of uredia present at the time of harvesting varied from 100 to 375.
6. J. H. Faull Herbarium nos. 7749–7750.

B. *From Abies balsamea to Athyrium angustum*

1. *Three inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 27 to July 31.
3. The experiments were harvested 23 to 27 days after inoculation.

C. *From Abies balsamea to Matteuccia Struthiopteris*

1. *Four inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 26 to July 31.
3. The experiments were harvested 23 to 28 days after inoculation.

D. *From Abies balsamea to Onoclea sensibilis*

1. *Three inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 26 to July 30.
3. The experiments were harvested 24 to 28 days after inoculation.

E. *From Abies balsamea to Osmunda Claytoniana*

1. *Two inoculation experiments* were made; both gave *negative* results.
2. The date of inoculation was July 27.
3. The experiments were harvested 27 days after inoculation.

5. **Uredinopsis Osmundae** Magnus

Uredinopsis Osmundae is known to occur in North America only. All three of the species of *Osmunda* growing in that part of the world, namely, *O. cinnamomea* L., *O. Claytoniana* L. and *O. regalis* var. *spectabilis* (Willd.) A. Gray, are susceptible to *U. Osmundae*. It is of interest to note that *U. Osmundae* has never been reported from Europe or Asia, although *O. regalis* L. is widely distributed in each of those continents.

Fraser (6) included *Uredinopsis Osmundae* in his life history studies of *Uredinopsis*. His efforts were restricted to carrying it over from *O. Claytoniana* to *Abies balsamea*, and in that he was successful. Fraser's work has been repeated here and extended to a comprehensive life history investigation of the rust in three series, each beginning with the rust from a different one of its three known fern hosts. For example, in one series overwintered telial material from *O. cinnamomea* was used in inoculating *Abies balsamea*. Next, the culturally produced aeciospores were sown on fronds of each of the three species of *Osmunda* mentioned above. Then the culturally produced urediospores from each of the fern species of these experiments were used to inoculate the other two species of *Osmunda*. Finally tests were made on fern species other than those of

Osmunda. The same program was followed in the two other series. Summaries of the experiments are recorded in Tables 9 to 21.

The main findings of the investigations are as follows:

(a) *Uredinopsis Osmundae* from *Osmunda cinnamomea, O. Claytoniana* and *O. regalis* var. *spectabilis* has *Abies balsamea* as an alternate host.

(b) Morphologically no distinctions are recognizable that can be correlated with the fern host origins of the rust. Throughout, on that basis, the rust is *U. Osmundae* Magnus.

(c) Some differences in developmental periods exist according to the fern origins of the rust and the ferns on which it is cultured. In certain instances these point to the existence of different biological strains; but more often they seem to indicate different degrees of host resistance.

(d) There are at least two biological strains of *U. Osmundae*. One of them is capable of causing infection of all three species of *Osmunda*. A second one infects *O. Claytoniana* and *O. regalis* var. *spectabilis*, but not *O. cinnamomea*.

(e) The following ferns are immune to *Uredinopsis Osmundae* — *Athyrium angustum* (Willd.) Presl, *Dryopteris Linnaeana* C. Chr., *Matteuccia Struthiopteris* (L.) Todaro, *Onoclea sensibilis* L.

TABLE 9.

CULTURES OF UREDINOPSIS OSMUNDAE
FROM OSMUNDA CLAYTONIANA TO ABIES BALSAMEA

1. *Forty-eight inoculation experiments* were made; forty-six gave *positive* results.
2. The dates of inoculation ranged from June 10 to July 1.
3. Yellowing of the needles appeared 10 to 14 days after inoculation. *The average was 12 days.*
4. The spermogonia were first observed 11 to 17 days after inoculation. *The average was 14 days.*
5. The peridermia were first observed 21 to 26 days after inoculation. *The average was 23 days.*
6. The peridermia usually began to rupture one to two days following their first appearance.
7. The production of peridermia was practically completed within 47 days after inoculation. *The average was about 30 days.*
8. The number of infected needles with peridermia varied from 0 to 157. *The average was 58.* One infection only produced no peridermia.
9. J. H. Faull Herbarium nos. 7713–7721 and 8430–8431.

TABLE 10.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA CLAYTONIANA ORIGIN) FROM ABIES BALSAMEA TO VARIOUS FERNS, USING AS INOCULUM AECIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 9.

A. *From Abies balsamea to Osmunda Claytoniana*

1. *Ten inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 8 to July 29.
3. Mature uredia were first observed 8 to 12 days after inoculation.
4. The experiments were harvested 11 to 19 days after inoculation. *The average was 15 days.*
5. The approximate number of uredia present at the time of harvesting varied from 150 to 1100. *The average was 390.*
6. J. H. Faull Herbarium nos. 7722–7724.

B. *From Abies balsamea to Osmunda regalis var. spectabilis*

1. *Nine inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 8 to July 29.
3. Mature uredia were first observed 10 to 17 days after inoculation.
4. The experiments were harvested 16 to 32 days after inoculation. *The average was 20 days.*
5. The approximate number of uredia present at the time of harvesting varied from 10 to 450. *The average was 185.*
6. J. H. Faull Herbarium nos. 7726–7728 and 8432–8433.

C. *From Abies balsamea to Osmunda cinnamomea*

1. *Ten inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 8 to July 29.
3. The experiments were harvested about 40 days after inoculation.

D. *From Abies balsamea to Athyrium angustum*

1. *Three inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 20 to July 25.
3. The experiments were harvested 29 to 33 days after inoculation.

E. *From Abies balsamea to Dryopteris Linnaeana*

1. *Four inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 16 to July 28.
3. The experiments were harvested 26 to 33 days after inoculation.

F. *From Abies balsamea to Matteuccia Struthiopteris*

1. *Four inoculation experiments* were made; all gave *negative* results.

2. The dates of inoculation ranged from July 17 to July 29.
3. The experiments were harvested 25 to 30 days after inoculation.

G. *From Abies balsamea to Onoclea sensibilis*

1. *Four inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 17 to July 28.
3. The experiments were harvested 26 to 33 days after inoculation.

TABLE 11.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA CLAYTONIANA ORIGIN) FROM OSMUNDA CLAYTONIANA TO VARIOUS FERNS, USING AS INOCULUM UREDIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 10 (A).

A. *From Osmunda Claytoniana to Osmunda Claytoniana*

1. *Three inoculation experiments* were made; all gave *positive* results. One control was slightly infected.
2. The dates of inoculation ranged from July 25 to July 31.
3. Mature uredia were first observed 8 to 12 days after inoculation.
4. The experiments were harvested 11 to 12 days after inoculation.
5. The approximate number of uredia present at the time of harvesting varied from 300 to 1400. *The average was 700.*
6. J. H. Faull Herbarium nos. 7725 and 8434–8435.

B. *From Osmunda Claytoniana to Osmunda regalis var. spectabilis*

1. *Four inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 25 to July 31.
3. Mature uredia were first observed 9 to 12 days after inoculation.
4. The experiments were harvested 13 to 17 days after inoculation.
5. The approximate number of uredia present at the time of harvesting varied from 90 to 700. *The average was 302.*
6. J. H. Faull Herbarium nos. 7729–7730 and 8432–8433.

C. *From Osmunda Claytoniana to Osmunda cinnamomea*

1. *Four inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 25 to July 31.
3. The experiments were harvested 22 to 38 days after inoculation.

TABLE 12.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA CLAYTONIANA ORIGIN) FROM OSMUNDA REGALIS VAR. SPECTABILIS TO VARIOUS FERNS, USING AS INOCULUM UREDIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 10 (B).

A. *From Osmunda regalis var. spectabilis to Osmunda Claytoniana*

1. *One inoculation experiment* was made; it gave *positive* results.
2. The date of inoculation was July 24.
3. Mature uredia were first observed 12 days after inoculation.
4. The experiment was harvested 13 days after inoculation.
5. The approximate number of uredia present at the time of harvesting was 1000.
6. J. H. Faull Herbarium no. 8438.

B. *From Osmunda regalis var. spectabilis to Osmunda regalis var. spectabilis*

1. *One inoculation experiment* was made; it gave *positive* results.
2. The date of inoculation was July 24.
3. Mature uredia were first observed 12 days after inoculation.
4. The experiment was harvested 15 days after inoculation.
5. The approximate number of uredia present at the time of harvesting was 250.
6. J. H. Faull Herbarium no. 8439.

C. *From Osmunda regalis var. spectabilis to Osmunda cinnamomea*

1. *Two inoculation experiments* were made; both gave *negative* results.
2. The date of inoculation was July 24.
3. The experiments were harvested 35 days after inoculation.

TABLE 13.

CULTURES OF UREDINOPSIS OSMUNDAE FROM OSMUNDA REGALIS VAR. SPECTABILIS TO ABIES BALSAMEA

1. *Twenty-five inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from June 13 to June 23.
3. Yellowing of the needles appeared 10 to 14 days after inoculation. *The average was 12 days.*
4. The spermogonia were first observed 11 to 16 days after inoculation. *The average was 13 days.*
5. The peridermia were first observed 20 to 26 days after inoculation. *The average was 23 days.*
6. The peridermia usually began to rupture the first or second day following their first appearance.
7. The production of peridermia was practically completed within 33 days after inoculation. *The average was about 28 days.*

8. The number of infected needles with peridermia varied from 1 to 78. *The average was 24.*
9. J. H. Faull Herbarium nos. 8440–8441.

TABLE 14.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA REGALIS VAR. SPECTABILIS ORIGIN) FROM ABIES BALSAMEA TO VARIOUS FERNS, USING AS INOCULUM AECIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 13.

A. *From Abies balsamea to Osmunda regalis var. spectabilis*

1. *Five inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 14 to July 20.
3. Mature uredia were first observed 9 to 13 days after inoculation.
4. The experiments were harvested 15 to 17 days after inoculation. *The average was 16 days.*
5. The approximate number of uredia present at the time of harvesting varied from 100 to 1100. *The average was 530.*

B. *From Abies balsamea to Osmunda Claytoniana*

1. *Five inoculation experiments* were made; all gave *positive* results. One control showed slight infection.
2. The dates of inoculation ranged from July 16 to July 20.
3. Mature uredia were first observed 10 to 11 days after inoculation.
4. The experiments were harvested 13 to 15 days after inoculation. *The average was 14 days.*
5. The approximate number of uredia present at the time of harvesting varied from 130 to 1000. *The average was 436.*

C. *From Abies balsamea to Osmunda cinnamomea*

1. *Six inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 14 to July 20.
3. The experiments were harvested about 40 to 43 days after inoculation.

TABLE 15.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA REGALIS VAR. SPECTABILIS ORIGIN) FROM OSMUNDA REGALIS VAR. SPECTABILIS TO VARIOUS FERNS, USING AS INOCULUM UREDIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 14 (A).

A. *From Osmunda regalis var. spectabilis to Osmunda regalis var. spectabilis*

1. *Two inoculation experiments* were made; both gave *positive* results.
2. The dates of inoculation were July 31 and August 5.

3. Mature uredia were first observed 12 and 14 days after inoculation.
4. The experiments were harvested 13 and 16 days after inoculation.
5. The approximate numbers of uredia present at the time of harvesting were 65 and 550.
6. J. H. Faull Herbarium nos. 8442–8443.

B. *From Osmunda regalis var. spectabilis to Osmunda Claytoniana*

1. *Two inoculation experiments* were made; both gave *positive* results.
2. The dates of inoculation were July 31 and August 5.
3. Mature uredia were first observed 12 days after inoculation.
4. The experiments were harvested 14 and 19 days after inoculation.
5. The approximate numbers of uredia present at the time of harvesting were 250 and 400.
6. J. H. Faull Herbarium nos. 8444–8445.

C. *From Osmunda regalis var. spectabilis to Osmunda cinnamomea*

1. *Three inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 31 to August 5.
3. The experiments were harvested 31 to 32 days after inoculation.

TABLE 16.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA REGALIS VAR. SPECTABILIS ORIGIN) FROM OSMUNDA CLAYTONIANA TO VARIOUS FERNS, USING AS INOCULUM UREDIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 14 (B).

A. *From Osmunda Claytoniana to Osmunda regalis var. spectabilis*

1. *Two inoculation experiments* were made; both gave *positive* results.
2. The dates of inoculation were July 29 and August 2.
3. Mature uredia were first observed 11 and 12 days after inoculation.
4. The experiments were harvested 13 and 15 days after inoculation.
5. The approximate numbers of uredia present at the time of harvesting were 120 and 500.
6. J. H. Faull Herbarium nos. 8446–8447.

B. *From Osmunda Claytoniana to Osmunda Claytoniana*

1. *Two inoculation experiments* were made; both gave *positive* results.
2. The dates of inoculation were July 29 and August 5.
3. Mature uredia were first observed 12 and 13 days after inoculation.
4. The experiments were harvested 13 and 15 days after inoculation.

5. The approximate numbers of uredia present at the time of harvesting were 500 and 1700.
6. J. H. Faull Herbarium no. 8448.

C. *From Osmunda Claytoniana to Osmunda cinnamomea*

1. *Three inoculation experiments* were made; all gave *negative* results.
2. The dates of inoculation ranged from July 29 to August 2.
3. The experiments were harvested 33 to 34 days after inoculation.

TABLE 17.

CULTURES OF UREDINOPSIS OSMUNDAE FROM OSMUNDA CINNAMOMEA TO ABIES BALSAMEA

1. *Forty inoculation experiments* were made; thirty-seven gave *positive* results.
2. The dates of inoculation ranged from June 14 to June 25.
3. Yellowing of the needles appeared 9 to 16 days after inoculation. *The average was 11 days.*
4. The spermogonia were first observed 10 to 16 days after inoculation. *The average was 12 days.*
5. The peridermia were first observed 19 to 27 days after inoculation. *The average was 22 days.*
6. The peridermia usually began to rupture about the second day following their first appearance.
7. The production of peridermia was practically completed within 38 days after inoculation. *The average was about 30 days.*
8. The number of infected needles with peridermia varied from 1 to 134. *The average was about 55.*
9. J. H. Faull Herbarium nos. 8449–8456.

TABLE 18.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA CINNAMOMEA ORIGIN) FROM ABIES BALSAMEA TO VARIOUS FERNS, USING AS INOCULUM AECIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 17.

A. *From Abies balsamea to Osmunda cinnamomea*

1. *Six inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 10 to July 24.
3. Mature uredia were first observed 11 to 16 days after inoculation. *The average was 13 days.*
4. The experiments were harvested 15 to 26 days after inoculation. *The average was 19 days.*
5. The approximate number of uredia present at the time of harvesting varied from 550 to 1700. *The average was 917.*

B. *From Abies balsamea to Osmunda Claytoniana*

1. *Six inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 10 to July 17.
3. Mature uredia were first observed 14 to 18 days after inoculation. *The average was 16 days.*
4. The experiments were harvested 17 to 24 days after inoculation. *The average was 21 days.*
5. The approximate number of uredia present at the time of harvesting varied from 2 to 18. *The average was 12.*

C. *From Abies balsamea to Osmunda regalis var. spectabilis*

1. *Eight inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 10 to July 23.
3. Mature uredia were first observed 11 to 16 days after inoculation. *The average was 13 days.*
4. The experiments were harvested 14 to 23 days after inoculation. *The average was 20 days.*
5. The approximate number of uredia present at the time of harvesting varied from 70 to 400. *The average was 183.*

TABLE 19.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA CINNAMOMEA ORIGIN) FROM OSMUNDA CINNAMOMEA TO VARIOUS FERNS, USING AS INOCULUM UREDIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 18 (A).

A. *From Osmunda cinnamomea to Osmunda cinnamomea*

1. *Two inoculation experiments* were made; both gave *positive* results.
2. The dates of inoculation were August 1 and August 9.
3. Mature uredia were first observed 17 days after inoculation.
4. The experiments were harvested 22 days after inoculation.
5. The approximate numbers of uredia present at the time of harvesting were 125 and 250.
6. J. H. Faull Herbarium no. 8457.

B. *From Osmunda cinnamomea to Osmunda Claytoniana*

1. *Two inoculation experiments* were made; both gave *positive* results. One produced teliospores only.
2. The dates of inoculation were August 1 and August 9.
3. Mature uredia were first observed 15 days after inoculation.
4. The experiments were harvested 19 and 28 days after inoculation.
5. The approximate numbers of uredia present at the time of harvesting were 35 and 0.
6. J. H. Faull Herbarium nos. 8458–8459.

C. *From Osmunda cinnamomea to Osmunda regalis var. spectabilis*

1. *Three inoculation experiments* were made; all gave *positive* results.
2. The date of inoculation was August 9.
3. Mature uredia were first observed 15 to 18 days after inoculation.
4. The experiments were harvested 23 days after inoculation.
5. The approximate number of uredia present at the time of harvesting varied from 50 to 225. *The average was 125.*
6. J. H. Faull Herbarium nos. 8460–8462.

TABLE 20.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA CINNAMOMEA ORIGIN) FROM OSMUNDA CLAYTONIANA TO VARIOUS FERNS, USING AS INOCULUM UREDIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 18 (B).

A. *From Osmunda Claytoniana to Osmunda cinnamomea*

1. *One inoculation experiment* was made; it gave *positive* results.
2. The date of inoculation was August 3.
3. Mature uredia were first observed 16 days after inoculation.
4. The experiment was harvested 20 days after inoculation.
5. The approximate number of uredia present at the time of harvesting was 43.
6. J. H. Faull Herbarium no. 8463.

B. *From Osmunda Claytoniana to Osmunda Claytoniana*

1. *One inoculation experiment* was made; it gave *positive* results.
2. The date of inoculation was August 3.
3. Mature uredia were first observed 16 days after inoculation.
4. The experiment was harvested 16 days after inoculation.
5. The approximate number of uredia present at the time of harvesting was 7.
6. J. H. Faull Herbarium no. 8464.

C. *From Osmunda Claytoniana to Osmunda regalis var. spectabilis*

1. *One inoculation experiment* was made; it gave *positive* results.
2. The date of inoculation was August 8.
3. Mature uredia were first observed 14 days after inoculation.
4. The experiment was harvested 17 days after inoculation.
5. The approximate number of uredia present at the time of harvesting was 80.
6. J. H. Faull Herbarium no. 8465.

TABLE 21.

CULTURES OF UREDINOPSIS OSMUNDAE (OF OSMUNDA CINNAMOMEA ORIGIN) FROM OSMUNDA REGALIS VAR. SPECTABILIS TO VARIOUS FERNS, USING AS INOCULUM UREDIOSPORES CULTURALLY PRODUCED IN THE EXPERIMENTS RECORDED IN TABLE 18 (C).

A. *From Osmunda regalis var. spectabilis to Osmunda cinnamomea*

1. *Three inoculation experiments* were made; all gave *positive* results.
2. The dates of inoculation ranged from July 30 to August 10.
3. Mature uredia were first observed 14 days after inoculation.
4. The experiments were harvested 14 to 21 days after inoculation.
5. The approximate number of uredia present at the time of harvesting varied from 250 to 800. *The average was 567.*
6. J. H. Faull Herbarium nos. 8466–8467.

B. *From Osmunda regalis var. spectabilis to Osmunda regalis var. spectabilis*

1. *Two inoculation experiments* were made; both gave *positive* results.
2. The dates of inoculation were July 30 and August 10.
3. Mature uredia were first observed 11 and 14 days after inoculation.
4. The experiments were harvested 13 and 22 days after inoculation.
5. The approximate numbers of uredia present at the time of harvesting were 100 and 60.
6. J. H. Faull Herbarium nos. 8468–8469.

C. *From Osmunda regalis var. spectabilis to Osmunda Claytoniana*

1. *Two inoculation experiments* were made; both gave *positive* results.
2. The dates of inoculation were July 30 and August 10.
3. Mature uredia were first observed 18 days after inoculation.
4. The experiments were harvested 20 and 22 days after inoculation.
5. The approximate numbers of uredia present at the time of harvesting were 19 and 10.
6. J. H. Faull Herbarium nos. 8470–8471.

6. **Uredinopsis ceratophora** Faull

A rust of the genus *Uredinopsis* has long been known to occur on *Cystopteris bulbifera* (L.) Bernh. It was originally identified as *U. Atkinsonii* Magnus and it has been carried along as a representative of that species with every subsequent change of nomenclature. But as Faull (3) has recently stated, "a comparative study of type specimens shows that it stands by itself as a distinctive, well-marked, heretofore

unnamed species." Moreover, he has shown that *U. longimucronata* Faull from *Athyrium angustum,* until now regarded as *U. Atkinsonii* Magnus, does not cause infection of *Cystopteris bulbifera.* So he has called it *Uredinopsis ceratophora.* Scant attention seems to have been given to this rust and until now nothing has been published on its life history. My culture work with *U. ceratophora* has been fragmentary; but sufficient was done to show that its life history follows the known Uredinopsis pattern. Using teliosporic material for inoculum it has been found that *Abies balsamea* serves as alternate host, but no reverse cultures were made. A summary of the experiments is recorded in Table 22.

TABLE 22.

CULTURES OF UREDINOPSIS CERATOPHORA FROM CYSTOPTERIS BULBIFERA TO ABIES BALSAMEA

1. *Seven inoculation experiments* were made; two gave *positive* results.
2. The date of inoculation was June 25.
3. The production of peridermia was completed within 40 days after inoculation.
4. The number of infected needles with peridermia varied from 6 to 12.
5. J. H. Faull Herbarium no. 9308.

III. DEVELOPMENTAL PERIODS

(a) Haploid phase

The haploid phase of all species of *Uredinopsis* of known life history, except *U. macrosperma,* is begun and completed on Abies needles of the current season. So far as my demonstrations go, it begins at the time of or soon after expansion of the needles and is well over before the end of August. How long the new needles remain susceptible was not determined; but the probability is that their period of susceptibility closely coincides with the normal time range of basidiospore production. This does not mean that the inner tissues of the needles ever acquire resistance, but rather that the epidermal defenses soon become adequate to resist entrance of the rust germ tubes.

After the inception of infection, the interval that elapses until the first fructifications make their appearance is relatively short. Thus, it was found that the first spermogonia were mature in 12 to 14 days on the average and the first peridermia in 20 to 23 days. Comparative developmental data are assembled in Table 23.

As for *U. macrosperma,* however, the haploid phase is of long duration — a year or more. It probably begins on young needles of the cur-

rent season, but peridermia do not develop until the affected needles are in their second year, and occasionally they are found on needles of the third to the fifth year. Although no direct experiments have been made this conclusion can be drawn fairly from field observations and the experiments of Weir & Hubert (14) in culturing *U. macrosperma* on *Pteridium aquilinum* var. *lanuginosum* (Bong.) Fernald. In that work they used as inoculum the aeciospores of *Peridermium pseudo-balsameum* (D. & H.) Arthur and Kern, a rust occurring only on needles of the second to the fifth year.

TABLE 23.

COMPARATIVE DEVELOPMENTAL DATA ON THE HAPLOID PHASE OF SPECIES OF UREDINOPSIS ON ABIES BALSAMEA.

Rust species	No. of expmts.	First appearance of spermogonia	Average	First appearance of peridermia	Average	Av. no. of infected needles per experiment
U. Struthiopteridis	49	10–15 days	12 days	19–24 days	21 days	37
U. mirabilis	39	10–15 days	12 days	21–28 days	23 days	27
U. longimucronata	53	9–18 days	12 days	17–25 days	20 days	52
U. Phegopteridis	14	10–15 days	12 days	21–23 days	23 days	34
U. Osmundae (of Osmunda Claytoniana origin)	46	11–17 days	14 days	21–26 days	23 days	58
U. Osmundae (of Osmunda regalis var. spectabilis origin)	25	11–16 days	13 days	20–26 days	23 days	24
U. Osmundae (of Osmunda cinnamomea origin)	37	10–16 days	12 days	19–27 days	22 days	55

The recognition of Uredinopsis species in the field is complicated by the fact that certain species of *Milesia*, also with white peridermia on *Abies*, often occur in the same localities along with them. Thus, two species of *Milesia*, namely *M. intermedia* Faull and *M. marginalis* Faull & Watson, characterized by peridermia on the first year needles of *Abies balsamea*, are abundant throughout the North American area in which the species of *Uredinopsis* of Table 23 abound; and in certain portions of the same region *M. fructuosa* Faull also occurs. The peridermia of these species are so like those of *Uredinopsis* that offhand generic recognition is perhaps impossible. But evident distinctions do reside in such

microscopic characters as minor spermogonial structures and the larger size of the aeciospores of the species of *Milesia*.

Comparing Table 23 on Uredinopsis rusts with the records published by Faull (3) on the biology of Milesian rusts, it is plain, however, that another distinction exists, namely, differences in the lengths of the developmental periods of the haploid phases of the compared species of the two genera. In the Uredinopsis species the spermogonia are mature within an average of 12 to 14 days, while in the Milesia species the average is 18–19 days. The comparable times up to maturity of the peridermia are 20 to 23 days for *Uredinopsis* and 34 to 43 days for *Milesia*. Thus the sequence of these white rusts on *Abies balsamea* under natural conditions is (1) *Uredinopsis,* (2) *Uredinopsis* and *Milesia,* (3) *Milesia*. Moreover, as the peridermia of the species of *Milesia* are quite persistent, they may be found up until late in the summer or even early fall, that is, until long after no trace of *Uredinopsis* remains.

(b) Diploid phase

The diploid phase of species of *Uredinopsis* can apparently be initiated on their fern hosts at any time after the fronds are fairly well expanded; and, once established, its mycelium continues to grow as long as the infected fronds are photosynthetically active. Primary inoculation is by means of aeciospores or overwintered urediospores. Secondary infections result from inoculation with urediospores of the ordinary type. In most species the developmental period up to the appearance of the first uredia is quite short. Table 24 presents comparative data for five of them.

TABLE 24.

COMPARATIVE DATA ON THE INITIAL DEVELOPMENT OF THE DIPLOID PHASE OF SPECIES OF UREDINOPSIS ON THEIR FERN HOSTS

A. *Using culturally produced aeciospores as inoculum.*

Rusts	No. of expmts.	First appearance of uredia	Average no. of uredia per expmt.
U. Struthiopteridis on Matteuccia Struthiopteris	6	10–11 days	138
U. mirabilis on Onoclea sensibilis	6	8–9 days	350
U. longimucronata on Athyrium angustum	11	16–30 days (av. 23 days)	88

TABLE 24 (Continued)

Rusts	No. of expmts.	First appearance of uredia	Average no. of uredia per expmt.
U. Phegopteridis on Dryopteris Linnaeana	3	7–8 days	258
U. Osmundae (of Osmunda Claytoniana origin)			
(a) on O. Claytoniana	10	8–12 days (av. 10 days)	390
(b) on O. regalis var. spectabilis	9	10–17 days (av. 13 days)	185
(c) on O. cinnamomea	10	*negative*	*negative*
U. Osmundae (of Osmunda regalis var. spectabilis origin)			
(a) on O. regalis var. spectabilis	5	9–13 days	530
(b) on O. Claytoniana	5	10–12 days	436
(c) on O. cinnamomea	6	*negative*	*negative*
U. Osmundae (of Osmunda cinnamomea origin)			
(a) on O. cinnamomea	6	11–16 days (av. 13 days)	917
(b) on O. regalis var. spectabilis	8	11–16 days (av. 13 days)	183
(c) on O. Claytoniana	6	14–18 days (av. 16 days)	12
B. *Using culturally produced urediospores as inoculum.*			
U. Osmundae (of Osmunda Claytoniana origin)			
(a) From O. Claytoniana to O. Claytoniana	3	8–12 days	700
(b) From O. Claytoniana to O. regalis var. spectabilis	4	9–12 days	302
(c) From O. Claytoniana to O. cinnamomea	4	*negative*	*negative*
(d) From O. regalis var. spectabilis to O. Claytoniana	1	12 days	100
(e) From O. regalis var. spectabilis to O. regalis var. spectabilis	1	12 days	250
(f) From O. regalis var. spectabilis to O. cinnamomea	2	*negative*	*negative*

TABLE 24 (Continued)

Rusts	No. of expmts.	First appearance of uredia	Average no. of uredia per expmt.
U. Osmundae (of O. regalis var. spectabilis origin)			
(a) From O. regalis var. spectabilis to O. regalis var. spectabilis	2	13–16 days	355
(b) From O. regalis var. spectabilis to O. Claytoniana	2	12 days	325
(c) From O. regalis var. spectabilis to O. cinnamomea	3	*negative*	*negative*
(d) From O. Claytoniana to O. Claytoniana	2	13–15 days	1100
(e) From O. Claytoniana to O. regalis var. spectabilis	2	13–15 days	310
(f) From O. Claytoniana to O. cinnamomea	3	*negative*	*negative*
U. Osmundae (of O. cinnamomea origin)			
(a) From O. cinnamomea to O. cinnamomea	2	17 days	188
(b) From O. cinnamomea to O. regalis var. spectabilis	3	15–18 days	125
(c) From O. cinnamomea to O. Claytoniana	2	15 days	19
(d) From O. regalis var. spectabilis to O. cinnamomea	3	14 days	567
(e) From O. regalis var. spectabilis to O. regalis var. spectabilis	2	11–14 days	80
(f) From O. regalis var. spectabilis to O. Claytoniana	2	18 days	15
(g) From O. Claytoniana to O. cinnamomea	1	16 days	43
(h) From O. Claytoniana to O. regalis var. spectabilis	1	14 days	80
(i) From O. Claytoniana to O. Claytoniana	1	16 days	7

From the data recorded in Table 24 several conclusions logically follow. (1) The developmental period for *U. longimucronata* on its fern host is notably longer than that of the other species on their respective fern hosts. (2) There are evidently two biological strains of *U. Osmundae;* one passes to all three species of *Osmunda; Osmunda*

cinnamomea is immune to the other strain. (3) *Osmunda regalis* var. *spectabilis* is a congenial host for both strains. (4) *Osmunda Claytoniana* is not a congenial host for the strain that parasitizes *O. cinnamomea*.

No efforts were made in my culture experiments to determine what length of time might elapse after inoculation before amphispores are formed. None developed in the cultures, but that was probably because they were harvested too soon.

Likewise no attempt was made to determine the length of the developmental period up to the time of the appearance of the first teliospores. Teliospores, however, did develop in five of the cultures of *Uredinopsis longimucronata* on *Athyrium angustum*. They were formed 23, 25, 26, 28 and 31 days, respectively, after inoculation made with aeciospores.

IV. HABITS OF SPORE PRODUCTION

(a) Spermatia

The spermatia of the species studied here are produced in abundance and they are discharged in a copious spermatial fluid. The discharge continues over many days. These phenomena are apparently correlated with the relatively large size of the spermogonia and the ample protection afforded them by the host tissues in which they are embedded.

(b) Aeciospores

The peridermia of the species of *Uredinopsis* cultured by me made their appearance in a week to two weeks after the spermatial discharge began. The average was found to be 11 days for *U. Struthiopteridis*, 11 days for *U. mirabilis*, 8 days for *U. longimucronata*, 10 days for *U. Phegopteridis*, and 10 to 11 days for *U. Osmundae*. The production of peridermia was practically complete 28 to 33 days after inoculation. The ripe peridermia ruptured at their apices and discharge of the aeciospores then began. Rupture usually occurred within one to two days after the peridermia were apparently mature.

These data, it will be seen, are quite different from those obtained for *Milesia* (Faull, 3). Thus, for *M. intermedia* Faull, the period of peridermial formation was found to be 16 days after spermatial discharge began, for *M. marginalis* it was 24 days, and for *M. polypodophila* 30 days. Moreover, the peridermia in those species did not rupture sooner than 3 or 4 days on the average after they were mature. Comparing also the discharge periods of the peridermia of Uredinopsis and Milesia species observed, they are much shorter in the former. While in *Uredinopsis* aeciospore production is entirely over before the end of the sum-

mer months, Faull records that "it has frequently been noted that peridermia of *M. intermedia* formed soon after the middle of August were shedding spores until towards the end of September."

(c) Urediospores

Following inoculation of the fern hosts, the ordinary uredia of the species cultured were not long in making their appearance. For *Uredinopsis Struthiopteridis* it was 10 to 11 days, for *U. mirabilis* 8 to 9 days, for *U. longimucronata* 16 to 30 days (23 days on the average), and for *U. Osmundae* 9 to 10 days. Rupture of the uredia of Uredinopsis species takes place at once after maturity and typically it is apical. In species on *Pteridium,* however, it is often lateral or subbasal. Unless the weather is too damp, the discharged spores adhere in long, more or less slender, white tendrils. The spores are immediately viable. They are provided with four germ pores, two near each pole, and on germination a germ tube, as was first demonstrated by Bell (1), may issue through each pore.

The amphisporic uredia, in such species as are characterized by them, occur on the same lesions as those that produce the ordinary uredia; but they are later in making their appearance. The occurrence of amphisporic uredia in one species as compared with another, or even for the same species, often exhibits interesting contrasts with respect to frequency and earliness of production. For example, in *U. Kameiana* they are so prevalent and their production so soon replaces that of ordinary uredia, that the latter are rarely well represented in collections. The opposite situation prevails in *U. virginiana.* In that species ordinary uredia abound and amphisporic uredia are infrequent. Differences within the same species are aptly illustrated by *U. longimucronata.* In cooler regions the amphisporic uredia are relatively uncommon and appear late in the season; in warmer localities they are often very abundant and develop quite early.

The amphispores are retained within their uredia until the following spring and they are not viable before that time. When, finally, discharge does take place, they may issue, as observed particularly for *U. ceratophora,* in more or less well defined tendrils.

(d) Teliospores and basidiospores

The teliospores of *Uredinopsis* are produced in profusion immediately under the lower epidermis of infected fronds and a few are located under the upper epidermis. They occur separately or in more or less broken crusts of indefinite extent within the subepidermal intercellular spaces. Their cells all lie close to, or more often in actual contact with, the

epidermis. Each spore cell possesses a single germ pore and it is located in the outer cell wall.

Teliospores are abundant for all species growing in regions in which *Abies* is native. But in other parts of the world, that is, in areas beyond the natural distribution of *Abies*, teliospores are rarely present.

Regarding the time of formation of teliospores in *Uredinopsis*, the misconception prevails that their production is postponed to the end of the growing season (cf. Pady, 13). The time, however, seems not to be governed by the seasonal period; more likely it is determined by a nutritional influence in the lesions. However that may be, I have often found them before midsummer has arrived. It may be added that in a few species the tendency to form teliospores is so pronounced that not only is their formation active in midsummer, but also that comparatively few or even no uredia may occur on the lesions. In all cases, of course, teliospore formation is completed by the end of the growing season and the spores overwinter in the dead host leaves.

The teliospores are not viable until after the winter's rest. In the succeeding spring, however, they germinate promptly under suitable conditions of warmth and moisture. A basidium quickly grows out from each cell through the epidermis. The aërial portion divides into four cells, each of which produces a single basidiospore.

V. HOST RESTRICTIONS

The haploid phase of Uredinopsis species seems to occur on *Abies* only. To that extent there is apparently a generic host restriction. But few tests or observations have been made with respect to specific host resistance or specific rust aggressiveness. The likelihood is, however, that just as in the case of *Milesia* and *Abies* (cf. Faull, 3) the majority of and perhaps all species of *Abies* are more or less susceptible to all species of *Uredinopsis*, and conversely that all species of *Uredinopsis* may be passed more or less easily to most or perhaps all species of *Abies*. At all events the following incidental results of experimentation point to the correctness of those conclusions: (1) *Uredinopsis Struthiopteridis* has been cultured on *Abies alba, A. balsamea* and *A. Mayriana;* (2) *U. ossaeiformis* has been cultured on *A. firma, A. Mayriana* and *A. sachalinensis;* (3) nine species of *Uredinopsis* have been cultured on *A. Mayriana,* namely, *U. Adianti, U. Athyrii, U. filicina, U. hirosakiensis, U. intermedia, U. Kameiana, U. ossaeiformis, U. Struthiopteridis* and *U. Woodsiae;* (4) seven species of *Uredinopsis* have been cultured on *A. balsamea,* namely, *U. Atkinsonii, U. ceratophora, U. longimucronata, U. mirabilis, U. Osmundae, U. Phegopteridis* and *U. Struthiopteridis;*

(5) there are no records of negative experiments to offset the conclusions expressed above.

The diploid phase of Uredinopsis species, on the other hand, seems to be very closely host restricted — usually to one host. A single species only, *U. glabra,* is recognized by the writer (4) as occurring on representatives of more than one fern genus; and but five others are recognized as occurring on more than one species of the same genus. But even in such cases the only efforts made to determine whether or not these rusts may comprise biological strains are those recorded for *U. Osmundae* in this paper. In that instance two biological forms have been demonstrated — one can infect three species of *Osmunda,* the other but two, and the host species concerned exhibit different relative degrees of susceptibility.

Fraser and Faull, however, have independently made some tests on the fern host restrictions of a few species of *Uredinopsis,* each choosing as experimental subjects ferns known to be susceptible to some species of *Uredinopsis.* In all cases close host restrictions were demonstrated.

Fraser's findings were as follows: (1) **Uredinopsis Struthiopteridis** from *Matteuccia Struthiopteris* does not infect *Dryopteris Linnaeana, Onoclea sensibilis, Osmunda Claytoniana.* (2) **U. mirabilis** from *Onoclea sensibilis* does not infect *Athyrium angustum, Dryopteris Linnaeana, D. Thelypteris* var. *pubescens, Osmunda Claytonia, O. regalis* var. *spectabilis.*

Faull's results were as follows: (1) **Uredinopsis Struthiopteridis** from *Matteuccia Struthiopteris* does not infect *Athyrium angustum, Dryopteris Linnaeana, Onoclea sensibilis, Osmunda Claytoniana.* (2) **U. mirabilis** from *Onoclea sensibilis* does not infect *Athyrium angustum, Dryopteris Linnaeana, Matteuccia Struthiopteris, Osmunda Claytoniana.* (3) **U. longimucronata** from *Athyrium angustum* does not infect *Cystopteris bulbifera, C. fragilis, Dryopteris Linnaeana, D. Thelypteris* var. *pubescens, Matteuccia Struthiopteris, Onoclea sensibilis, Osmunda Claytoniana.* (4) **U. Phegopteridis** from *Dryopteris Linnaeana* does not infect *Athyrium angustum, Matteuccia Struthiopteris, Onoclea sensibilis, Osmunda Claytoniana.* (5) **U. Osmundae** from *Osmunda Claytoniana* does not infect *Athyrium angustum, Dryopteris Linnaeana, Matteuccia Struthiopteris, Onoclea sensibilis.*

VI. ECONOMIC CONSIDERATIONS

Uredinopsis not infrequently occurs so abundantly on firs that considerable injury to them must surely result. This would apply particularly to seedlings and young saplings. But so far as I am aware,

Kamei (11) is the only one to have made statistical studies of any kind on that topic. He made a detailed analysis of the effect of *U. hirosakiensis* on seedlings of *Abies Mayriana* growing in nursery plots. He found that infected plants in the plots varied from 12 to 58.7% of the total and that the number of infected needles per seedling varied from one to eleven. Obviously under such circumstances attention should be paid to the fern population adjacent to a nursery in which firs are grown. It is apparent, too, that studies on the influence of *Uredinopsis* on the natural reproduction of *Abies* in the forest might yield some interesting results.

The injurious effects of *Uredinopsis* on ferns are often very severe. They might conceivably be matters of concern to owners of properties in regions in which firs and ferns occur and in which the latter are of ornamental value. Thus, in such cases, *Athyrium angustum, Matteuccia Struthiopteris* and species of *Osmunda* frequently become unsightly by midsummer as a result of Uredinopsis infection. Probably the resultant injuries could largely be prevented by adopting means known to be effective in controlling rust diseases in other kinds of plants.

SUMMARY

1. Species of *Uredinopsis* in their diploid phase are known on *Osmunda* of the Osmundaceae and twelve genera of the Polypodiaceae, namely, *Adiantum, Athyrium, Blechnum, Cheilanthes, Cystopteris, Dryopteris, Matteuccia, Onoclea, Pellaea, Pteridium, Woodsia, Woodwardia.* The haploid phase occurs in nature or has been obtained by culturing on *Abies alba, A. balsamea, A. firma, A. grandis, A. Mayriana, A. sachalinensis.*

2. The life histories of sixteen of the twenty-five recognized species of *Uredinopsis* (cf. Faull, 4) have been demonstrated by culturing. This paper records detailed studies on the life histories of *U. ceratophora, U. longimucronata, U. mirabilis, U. Osmundae, U. Phegopteridis* and *U. Struthiopteridis.*

3. Teliospores are known for all of the twenty-five recognized species of *Uredinopsis* except *U. investita* and *U. Mayoriana.*

4. Data on the developmental periods of the species experimentally studied by the writer, up to the times the spermogonia and the peridermia first appear, are summarized in Table 23, and on the periods up to the first appearance of the uredia in Table 24.

5. Teliospore formation may begin as early as midsummer. The important determining factor is probably nutritional rather than seasonal.

The teliospores overwinter in dead infected fronds and first become viable in the following spring.

6. There is incidental evidence in support of the assumption that most, if not all, species of *Abies* are more or less susceptible to all species of *Uredinopsis,* and conversely that all species of *Uredinopsis* may be passed more or less easily to most or perhaps all species of *Abies.* But these conclusions await direct investigation.

On the other hand, it is reasonably certain that the species of *Uredinopsis* are closely restricted as to their fern hosts. This has been indicated by Fraser's experiments with *U. mirabilis* and *U. Struthiopteridis* and by my own experiments with *U. longimucronata, U. mirabilis, U. Osmundae, U. Phegopteridis* and *U. Struthiopteridis.*

7. It has been demonstrated here that *U. Osmundae* comprises two biological strains, one of them infecting three species of *Osmunda* and the other *O. Claytoniana* and *O. regalis* var. *spectabilis* only.

8. Economically, Uredinopsis rusts are of some importance in relation to both firs and ferns.

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I am under deep obligation, gratefully acknowledged, to Dr. E. H. Bensley for competent and devoted assistance in culturing *Uredinopsis longimucronata, U. mirabilis, U. Osmundae, U. Phegopteridis* and *U. Struthiopteridis,* and to Professor E. H. Moss for assistance in making some preliminary cultures.

LITERATURE CITED

1. Bell, H. P. Fern rusts of Abies. (Bot. Gaz. **77**: 1–31. 1924.)
2. Faull, J. H. Taxonomy and geographical distribution of the genus Milesia. (Contr. Arnold Arb. **2**: 1–138. 1932.)
3. ———— The biology of Milesian rusts. (Jour. Arnold Arb. **15**: 50–85. 1934.)
4. ———— Taxonomy and geographical distribution of the genus Uredinopsis. (Contr. Arnold Arb. **11**: 1–120. 1938.)
5. Fraser, W. P. Cultures of heteroecious rusts. (Mycologia, **4**: 175–193. 1912.)
6. ———— Further cultures of heteroecious rusts. (Mycologia, **5**: 233–239. 1913.)
7. ———— Notes on Uredinopsis mirabilis and other rusts. (Mycologia, **6**: 25–28. 1914.)
8. Kamei, S. On the life history of Uredinopsis Pteridis with special bearing on its peridermial stage. (Ann. Phytopath. Soc. Japan, **2**: 207–228. 1930.)
9. ———— On new species of heteroecious fern rusts. (Trans. Sapporo Nat. Hist. Soc. **12**: 161–174. 1932.)

10. ——— Genetic relation between some Japanese species of the fern rusts and the peridermia on firs. (Abstract) (Jour. Soc. Agric. & For. Sapporo, **24**: 364–365. 1933.)
11. ——— Identification of a peridermial stage on the seedlings of Abies Mayriana and the injury caused thereby. (Trans. Sapporo Nat. Hist. Soc. **13**: 153–161. 1934.)
12. KLEBAHN, H. Kulturversuche mit Rostpilzen, XVI. (Zeit. Pflanzenkr. **26**: 257–277. 1916.)
13. PADY, S. M. Teliospore development in the Pucciniastreae. (Canadian Jour. Res. **9**: 458–485. 1933.)
14. WEIR, J. R. & E. E. HUBERT. Observations on forest tree rusts. (Am. Jour. Bot. **4**: 327–335. 1917.)

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